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BOOKS AND LITERATURE

Die Chromosomenzahl von Zea Mays L. Ein Beitrag zur Hypothese der Individualität der Chromosomen und zur Frage über die Herkunft von Zea Mays L.[1] By YOSHINARI KUWADA.

The author of the paper, the title of which appears above, has well summed up his purpose in the subheading. As this article reports investigations of considerable cytological importance in a publication which is not likely to have wide circulation in America, it was thought advisable to review it at some length.

As Professor Kuwada clearly and concisely states his results and conclusions in his summary a translation is given below.

1. The chromosome number of *Zea Mays* L. is 10 (when the diploid number is 20). In forms either closely related systematically or supposedly ancestral types the chromosome number in the root tips is in general constantly 20 (seldom does the number approach the octoploid number).

2. It has been found that in one race of sugar corn which I received from the Agricultural Faculty of the Imperial University of Tokyo the chromosome number is different in different individuals. In the roots tips 21, 21, 22, 23 and 24 chromosomes were found. The number of tetrads is correspondingly different, namely, 10, 11 and 12. There is no relation between the chromosome number and the chemical nature of the endosperm.

3. Through a parallel study of the number and size of the tetrads and the length of the chromosomes in the root tips it has been shown that the number of chromosomes is increased through the cross fragmentation of certain chromosomes.

4. The measurement of the chromosome length in the root tips and the unequal lengths of the component elements of the tetrads allow us to draw the important conclusion that *Zea Mays* is of hybrid nature, and indeed, as Collins has rightly said, a hybrid between Euchlæna and an unknown plant of the Andropogoneæ.

5. The chromosomes supposedly derived from *Euchlœna* are longer than those coming from the Andropogoneæ species, so that the tetrads under certain circumstances are made up of elements of different lengths. The two chromosomes of the first kind A—B[2] and C—D have

[1] *Jour. of the Col. of Science*, Imp. Univ. of Tokyo, Vol. 39, Art. 10, 1919.

[2] It has been necessary for convenience to take some liberties with the method used by Kuwada for expressing his idea of the potentiality of fragmentation possessed by the various chromosomes. Here a solid dash be-

an inclination to fragment easily under certain conditions while the corresponding chromosomes of the latter type $\underline{a\ b}$ and $\underline{c\ d}$ do not show this tendency. In one plant (sugar corn) from the agricultural faculty of the University of Tokyo the chromosomes A—B and C—D have each cross fragmented into two chromosomes $\underline{A}$ $\underline{B}$ and $\underline{C}$ $\underline{D}$ and this condition is morphologically and genetically fixed. We therefore have three kinds of corresponding chromosomes: the cross-fragmented chromosomes, those having a tendency to fragment and those in which both of these characteristics are lacking.

6. In the formation of the tetrads the chromosomes $\underline{A}$ $\underline{B}$ and $\underline{C}$ $\underline{D}$ are dominant to A—B and C—D and recessive to $\underline{a\ b}$ and $\underline{c\ d}$. The dominance in the first case is somewhat unstable, so that the number of tetrads is subjected to fluctuation within certain limits. The difference in the behavior of the corresponding chromosomes A—B, C—D and $\underline{a\ b}$, $\underline{c\ d}$ to $\underline{A}$ $\underline{B}$ $\underline{C}$ $\underline{D}$ is also a point in favor of Collins' hypothesis.

7. If the chromosomes $\underline{A}$ $\underline{B}$ and A—B form a tetrad in the reduction division four combinations result: $\underline{A}$ $\underline{B}$, $\underline{A}$—B, A—$\underline{B}$ and A– –$\underline{B}$. The corresponding ends of the chromosomes A– and –B fuse relatively easily to reform the chromosome A—B. The possibility of fusion depends absolutely on the proximity of the corresponding ends of the passive cross-fragmented chromosome A– and –B. In this respect the parallel arrangement of the homologous chromosomes in the somatic cells is of great importance. The chromosomes $\underline{A}$ and –B or A– and $\underline{B}$ which would otherwise occasionally fuse to form the chromosome $\underline{A}$ and –B or A– and $\underline{B}$ remain sometimes as $\underline{A}$ and –B or A– and $\underline{B}$: the result being the variation in the number of the chromosomes. Two kinds of gametes occur, in one the chromosome number is constant and in the other it varies. The chromosomes in the first instance have the formula $\underline{A}$ $\underline{B}$ (number of chromosomes above normal) or A—B (normal number of chromosomes), and in the latter instance $\underline{A}$—B or A– $\underline{B}$ or occasionally A– –B. When the chromosomes $\underline{A}$ $\underline{B}$ and $\underline{a\ b}$ form a tetrad the result is very simple in that only two combinations are possible—$\underline{A}$ $\underline{B}$ and $\underline{a\ b}$. In these cases the number of chromosomes is constant. The union of $\underline{A}$ and $\underline{B}$ is only a phenomenon ascribed to the presence of $\underline{a\ b}$.

The empirical results agree with those developed from theoretical considerations based on the laws of chance.

8. The applicability of the laws of chance to the chromosome num-

tween two letters indicates a weak place that may easily break, a broken dash before or after a letter suggests a free end of a fragment which will link up with the suitable end of another fragment if opportunity offers, underscored single letters have no power of uniting (no free ends), while the binding together of two letters by underscoring represents a chromosome which can never fragment.

ber and the constancy of the true length of the chromosomes in the hybrids is a contribution favoring the individuality hypothesis.

9. The nuclear and cell size is dependent on the chromosome size and on the other hand the latter is modified by the cell size.

According to Kuwada there are two hypotheses concerning the origin of *Zea Mays* L. Iltis (1911) first suggested that this modern form might have been derived from some unknown tribe of Andropogoneæ, while Collins in 1912 put forward the claim that *Zea Mays* L. was a hybrid between an unknown species of the Andropogoneæ and *Euchlæna*.

In his cytological studies Kuwada finds that in species of *Euchlæna* and *Andropogoneæ* the chromosome number is the same as in *Zea Mays* L.—namely 20. In only one of the investigated groups of plants belonging to the *Andropogoneæ* was the chromosome number above 20, which places this particular species beyond consideration. The measurement of the chromosomes in a *Euchlæna* from south Florida shows that their total length is greater than is the case in *Andropogon Nardus* L. var. *Georingin* Hack. The respective total chromosome lengths in each case are given as 188.25 mm. and 111.3 mm.

Kuwada gives the results of a large number of measurements of the chromosomes in various varieties of maize taken at random or from plants in which the cytological conditions have been studied in the parental, F_1 and F_2 generations. His conclusion that the figures indicate that two length types of chromosomes are concerned in the modern plant do not seem to the present writer to be entirely born out by the facts.

In the measurement of chromosomes previous studies have shown that complexes from the same individual in the same or in different parts of the structure may show considerable variation in the total length of their component chromosomes. In general, of course, small cells will have smaller chromosomes and larger cells, larger chromosomes, but even in similar tissues very appreciable differences may occur. These variations are obviously due both to internal and to external causes. Fluctuation in the climatic or nutritive conditions may affect growth and vigor, while the volume of the cell imposes limitations on the size of the contained chromosomes. It has been shown by the present writer[3] that, be the total length of a complex long or short, the

[3] Hance, R. T., 1917, "The Diploid Chromosome Complexes of the Pig (*Sus scrofa*) and their Variations, *Jour. Morph.*, Vol. 30. 1918*a*, "Variations in the Number of Somatic Chromosomes in *Œnothera scintillans* De-

individual pairs always bear the same relation to each other, allowing the conclusion that whatever influences the size of the chromosomes generally affects all similarly. The figures of Kuwada bear out these observations very well. As pointed out above, his interpretation of his work seems somewhat forced. He recognizes the factors playing rôles in the behavior of the chromosomes, but does not feel that his results can be entirely explained by them.

To illustrate what is meant by the above criticism let us consider a cross made by Kuwada between sugar corn $22_{(15)}$ and Black Mexican $58_{(15)}$, another sugar corn. In both, dividing cells from adventitious roots were uniformly selected. The former has chromosome complexes averaging 149.05 mm. in length while the latter gives a total of 172.17 mm. This to Kuwada indicates a real and genetic difference in chromosome length, although in the same Black Mexican plant $58_{(15)}$ complexes from side root tips average only 145 mm. in length. This would signify that the length 172.11 was no more fundamental in plant $58_{(15)}$ than was 145, and lessens the weight of the evidence that the higher number betokens genetic chromosome differences with the length 149.05 in plant $22_{(15)}$. When the two plants are crossed the chromosome lengths in the hybrids are almost exactly one half of the sum of the lengths of these structures in the parents if 172.17 is accepted as the typical complex length for plant $58_{(15)}$—$1/2(149.05 + 172.17) = 160.61$. It may be pointed out here that one half the sum of the complex length found in the various roots of plant $58_{(15)}$ also closely approximates the same figure—$1/2(172.17 + 145) = 158.58$. The F_1 plants from the above cross possess sets of chromosomes whose length is very close to that expected on Kuwada's assumption of 149.05 and 172.17 as the basic or typical lengths of the parental chromosomes. The chromosomes in the F_1 plants varied from 155.75 mm. to 168.9 mm. and averaged 161.86 mm. This number fits in well with the anticipated result and at first would seem to justify the consideration of 172.17 mm. as the representative length for plant $58_{(15)}$. However, the chromosomes in the F_1 offspring were found in cells in the radicles of seed germinated in moist saw dust. The chromosomes in this early root tip in many forms are not infrequently larger than are found in the growing parts of

Vries, *Genetics*, Vol. 3. 1918*b*, "Variations in Somatic Chromosomes," *Biol. Bull.*, Vol. 35.

the older plant and Kuwąda's figures and statements show that maize is no exception to the general rule. This tendency for the chromosomes in the radicle to be larger puts a fictitious value on their measurements in this organ for comparison with the dimensions of chromosomes found elsewhere in the plant. As a matter of fact, in the number of examples given the average length of the chromosomes in all the plants is only a trifle more than one per cent. shorter than the similar data in regard to the chromosomes of the radicle, which difference would not greatly affect the end result. In this instance, although the physiological location of the chromosomes was undoubtedly one factor in determining their size, objection on this ground alone to the submission of the records of the F_1 chromosome lengths in substantiating the figure 172.17 as the fundamental chromosome length for plant $58_{(15)}$ would not seem to be entirely valid. However, to base a broad conclusion on the lengths of the chromosomes found in a particular part of a plant, even though comparing them with chromosomes from similar parts of other plants, is likely to obscure the real condition.

As has been shown in plant $58_{(15)}$, lengths of 172.17 mm. and 145 mm. were found. That these are not fixed lengths for the particular tissues concerned in this variety of corn is shown by the data given for other plants of the variety Black Mexican, in which lengths vary (for corresponding tissues) from 132.5 mm. to 181.25 mm., the average being 159.32 mm. There can be little question that the variety Black Mexican, as long as it is genetically pure, can have anything but comparable sets of chromosome throughout, holding in mind that though the lengths may vary the inter-pair relationship remains constant. Less variation in chromosome length is shown for the three plants of the variety "Sugar Corn" which were studied. The range of averages here is from 147.8 mm. to 151.6 mm.

Lastly, if real differences between the lengths of the chromosomes in plants $58_{(15)}$ and $22_{(15)}$ exist greater differences between the members of the pairs that are found in the hybrid offspring would be expected. Actually these elements mate up well as to length and if unequal homologous chromosomes have entered the zygotes union in a common environment has regulated their proportions. As the dimensions of the chromosomes are in part a function of their environment the selection as typical of any one complex or of even the average of com-

plexes from certain tissues only is not justified, considering our present ignorance of chromosome volume.

In support of the difference in length between the homologues of chromosome pairs as indicative of the genetic length types which Kuwada believes he has demonstrated he publishes drawings of tetrads showing the unequal length of the component elements. Personally I do not think that the figures are necessarily conclusive proof, since the arrangement of the homologues in several cases suggests a possible foreshortening, making the true length doubtful, and in other instances the drawings may well represent an entirely different form or stage of the tetrad. It is not the intention of this criticism to convey the impression that the investigator's figures fail absolutely in proving his point concerning the uneven length of the homologues, but rather to indicate that the illustrations are not nearly as satisfactory and as conclusive as those given in the publications of Wenrich[4] and Carothers[5] for somewhat similar conditions in other forms.

Between the *Euchlæna* and Andropogoneæ studied chromosome length differences appear which can scarcely be accounted for on the basis of environment. Since the characteristics of *Zea Mays* L. are intermediate between these forms the hope is raised that two sets of chromosomes will be found in the modern species, which hope the reviewer does not think has been realized. Indeed, though recognizing the evolutionary position of *Zea Mays* L. as given by some taxonomists, he offers the suggestion that in his opinion the present investigation has not, as far as the chromosomes are concerned, excluded the possibility of the origin by mutation of *Zea Mays* L. from *either Euchlæna* or the Andropogoneæ. A knowledge of the behavior of the chromosomes of these two forms in hybrids would be interesting and important.

In explanation of the variation in the number of chromosomes which Kuwada found in certain lines (20 to 24 chromosomes) he devised an exceedingly ingenious scheme which apparently thoroughly accounts for the numbers of chromosomes occurring in the offspring. It operates on the laws of chance and its theory

[4] Wenrich, D. H., 1916, "The Spermatogenesis of *Phrynotettix magnus* and the Individuality of the Chromosomes, *Bull. Mus. Comp. Zool.*, Harvard College, Vol. 60.

[5] Carothers, E. E., 1913, "The Mendelian Ratio in Relation to Certain Orthopteran Chromosomes," *Jour. Morph.*, Vol. 24.

seems to be completely justified by the results. As this explanation is adequately outlined in the translated summary further space need not be devoted to it.

The investigator's theory of factors located in each chromomere which govern the form of the chromosome, while convenient in explaining the cause of the reunion of the chromosome fragments in maize, is scarcely necessary. Chromosomes are not inherited as are the determiners for adult characteristics in the form of minute chemical forerunners, but are passed on complete in all respects. Consequently, factors to determine their form in the next generation are not needed—the chromosome itself is carried over. The actual form of the chromosome has been shown by McClung, Wenrich, Carothers and others to be determined largely by the location of the spindle fiber attachment.

It is considered that the reviewed report has not clearly demonstrated the origin of *Zea Mays* L. by means of chromosome measurements for the following reasons:

1. The length of the selected chromosome complexes in the forms particularly studied are not typical of the plant and such selection gives a false impression of the actual conditions.

2. The figures illustrating the length differences of the homologues composing the tetrads are not entirely convincing or satisfactory.

3. If two types of genetically fixed chromosome lengths exist in maize we would expect to find an expression of this difference when both types enter into the same individual. As far as the reviewer's interpretation of the tables of length is concerned, this difference does not exist in the F_1 plants.

Though there are reasons for not considering that Kuwada has proved his claims of the origin of *Zea Mays* L. he, nevertheless, is to be sincerely congratulated on an excellent cytological contribution involving great labor and care. To the reviewer the apparent failure of Professor Kuwada to demonstrate his main thesis dwindles in importance when the value of the "side issues" of the investigation are considered. His work on *Zea Mays* L. presents the following data:

1. The chromosome pairs of a complex may be arranged in a graduated length series and between each pair there is an approximately equal difference in length.

2. The genetic relation of the chromosomes is shown in parent and offspring.

3. When chromosomes fragment in *Zea Mays* L. it is the longer ones that are affected. These fragments may also fuse, causing variability in the total chromosome number.

4. Suggestive methods of studying chromosomes have been devised.

5. *Fragmentation* has been accounted for on the basis of genetic tendencies and the variable number of the chromosomes in the offspring of certain plants has been ingeniously explained with the aid of the device described in his summary.

The first four points (with the exception of the latter part of the third, which has not been observed) agree perfectly with the reviewer's earlier work on the Œnotheras and the pig. As to the fifth point, he has never found fragmentation in the germ line.

Difficulties of interpretation in metrical studies of chromosomes arise from a lack of standards, *i.e.*, knowledge of the limits of variation that chromosomes of a given form will show under many conditions and of the uncertainty introduced by the personal equation involved in drawing and measuring. With the hope of deriving such standards the present writer is at work on a plant and an animal possessing very few chromosomes. The usefulness of the information drawn from such studies has been elsewhere discussed.

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